Published in final edited form as:
Psychol Sci. 2012 October 1; 23(10): 1224–1232. doi:10.1177/0956797612441951.

A Time-Based Account of the Perception of Odor Objects and Valences

Jonas K. Olofsson[1,2], **Nicholas E. Bowman**[1], **Katherine Khatibi**[1], and **Jay A. Gottfried**[1]
[1]Department of Neurology, Feinberg School of Medicine, Northwestern University

[2]Department of Psychology, Stockholm University

Abstract

Is human odor perception guided by memory or emotion? Object-centered accounts predict that recognition of unique odor qualities precedes valence decoding. Valence-centered accounts predict the opposite: that stimulus-driven valence responses precede and guide identification. In a speeded response time study, participants smelled paired odors, presented sequentially, and indicated whether the second odor in each pair belonged to the same category as the first (object evaluation task) or whether the second odor was more pleasant than the first (valence evaluation task). Object evaluation was faster and more accurate than valence evaluation. In a complementary experiment, participants performed an identification task, in which they indicated whether an odor matched the previously presented word label. Responses were quicker for odors preceded by semantically matching, rather than nonmatching, word labels, but results showed no evidence of interference from valence on nonmatching trials. These results are in accordance with object-centered accounts of odor perception.

Keywords

olfactory perception; object recognition; emotions; naming; response time

An airborne smell possesses many different perceptual attributes, each of which carries a unique meaning for the smeller. Decoding these attributes—including odor valence and object quality (the perceptual basis of odor identification)—is critical for the olfactory system to guide appropriate behavioral responses, and both humans and other animals can easily discriminate these aspects of an odor stimulus. What remains less clear is how these perceptual features unfold in time. Are they processed serially, or in parallel? If they are processed serially, does the evaluation of an odor's pleasantness precede or follow the evaluation of the odor's quality? Answers to such questions have fundamental implications for neurobiological and psychological models of olfactory perception.

Two opposing models, one emphasizing the primacy of odor objects (*object-centered approach*) and the other emphasizing the primacy of odor valence (*valence-centered*

Corresponding Author: Jonas K. Olofsson, Department of Neurology, Feinberg School of Medicine, Northwestern University, 303 E. Chicago Ave., Chicago, IL 60611, jonas.olofsson@psychology.su.se.

Declaration of Conflicting Interests
The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Supplemental Material
Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

approach), have been put forward to explain the generation of olfactory perceptual experiences (Fig. 1a; for reviews, see Gottfried, 2010; Stevenson & Boakes, 2003; Wilson & Stevenson, 2003; Yeshurun & Sobel, 2010). According to the object-centered approach, representations of odor objects are activated by comparing olfactory inputs with memory templates early in the processing sequence (Stevenson & Boakes, 2003; Wilson & Stevenson, 2006). Such activation, in turn, triggers affective systems to produce an emotional response. Recent studies provide support for the existence of objects in olfaction (Gottfried, 2010; Stevenson & Wilson, 2007; Wilson & Stevenson, 2006), but their relevance for evaluations of valence has not been empirically addressed.

A widely held view is that olfaction is an intrinsically valence-driven sensory system. According to the valence-centered approach, information on odor identity has to be reconstructed from the valence response (Haddad et al., 2010; Khan et al., 2007; Yeshurun & Sobel, 2010). Supporting this viewpoint is the finding that valence tends to dominate olfactory perception (Khan et al., 2007; Lawless, 1989; Schiffman, Musante, & Conger, 1978). Even Plato believed that "the varieties of smell have no name, … but they are distinguished only as painful and pleasant" (Plato, trans. 2009, p. 147). It has even been suggested that an odorant's valence is essentially written into its physicochemical composition (Khan et al., 2007).

The object-centered and valence-centered accounts yield fundamentally different predictions about the temporal unfolding of olfactory perception (Fig. 1a). In an object-centered model, the time needed to identify or categorize an odor on the basis of its unique quality should be faster than the time needed to identify or categorize its hedonic attributes; a valence-centered model would make the opposite prediction. Moreover, in an object-centered model, variation in odor identification or categorization times should predict variation in valence evaluation times on an odor-by-odor basis, as valence is delayed by the activation of the representation of the odor object. In contrast, the valence-centered account holds that odor identification is intrinsically difficult because of a tenuous semantic linkage between valence evaluations and specific odor names (Yeshurun & Sobel, 2010). As a consequence, semantic interference in odor identification should be observed when the perceiver is given a verbal cue for odors that are similar in valence to a target odor. Semantic interference causes delayed response times for visual stimuli (Klein, 1964; Smith & Magee, 1980) and would be expected to do the same for odor stimuli.

In two experiments, we used speeded two-alternative forced-choice tasks to test these predictions. In Experiment 1 (Fig. 1b), participants made binary evaluations of serially presented odors, reporting either whether the second odor in each pair was in the same category as the first or whether it was more pleasant than the first. This design permitted a direct time-based comparison of object-centered and valence-centered olfactory perceptual decisions. In Experiment 2, we tested whether object-specific or valence-specific template cues are used to identify odors by having participants perform an identification task in which they decided whether each presented odor matched a preceding word label. Our findings indicate that odor object evaluations precede and predict odor valence evaluations, and that object templates support odor identification. These results strongly align with object-centered models of human olfactory perception.

Experiment 1

Method

Participants—Eight women and 6 men (mean age = 26.8 years, *SD* = 5.6 years) participated in this experiment. They reported no history of cigarette smoking, breathing problems, allergies, asthma, smell or taste problems, or neurological or psychiatric illness.

Participants provided informed consent to take part in the study, which was approved by the Northwestern University institutional review board.

Materials—A laptop computer was used to present sniff cues, binary response options, and analogue rating scales. The computer also triggered delivery of odorants through an air-dilution olfactometer (Johnson & Sobel, 2007; Zelano, Mohanty, & Gottfried, 2011) and recorded responses and response times (RTs) from keyboard button presses. Participants wore a nasal mask for odor delivery (Phantom nasal mask, Sleepnet Corp., Hampton, NH) and a pair of breathing belts (Siemens, Erlangen, Germany) that were used to record respiratory patterns during olfactory presentations (Plailly, Howard, Gitelman, & Gottfried, 2008). Eight odorants were selected from four odor object categories that varied in valence: pleasant floral odors (rose, lilac), pleasant minty odors (peppermint, wintergreen), unpleasant fuel odors (diesel/motor oil, gasoline), and unpleasant fish odors (sardine, fish flavor). Some odorants were obtained directly from their natural products (sardine oil, diesel/motor oil, gasoline), and others were obtained as flavors (fish), essential oils (rose, lilac, peppermint), or monomolecular compounds (wintergreen: methyl salicylate). Baseline ratings of these odors were obtained from the participants prior to the main experiment (scores were averaged across three ratings). These ratings confirmed that the participants accurately classified the odors as belonging to floral, minty, fuel, and fish categories, respectively, and that the odors differed predictably in valence (Figs. 2a and 2b).

Procedure—Participants made two consecutive sniffs on each trial, and were instructed to judge whether the odor presented on the second sniff belonged to the same object category as the odor presented on the first sniff (object evaluation task) or whether the second odor was more pleasant than the first odor (valence evaluation task). In this way, participants were always provided with a reference stimulus (the first odor) as the basis for their evaluation of the second odor. Sequential sniffs were separated by a delay of 4 s, and the intertrial interval was 11 s. Odor delivery was synchronized with the sniff cue (red cross-hair) and lasted for 1,000 ms. Stimulus pairs were arranged such that the second odor belonged to the same object category as the first odor on 50% of the trials (on the remaining trials, the second odor was drawn from the other categories in equal proportions), and the second odor was more pleasant than the first odor on 50% of trials; these constraints ensured that there were no inherent stimulus or response differences between the tasks. There were four object evaluation blocks and four valence evaluation blocks, with 24 trials in each block; block types were presented in alternation, and block order was counterbalanced across participants. Only responses from 200 to 5,000 ms following onset of the second sniff cue were considered for analyses.

Note that because the task involved cued sniffing, experimental noise in the RTs would have arisen mainly from between-participants variation in sniff onset, as opposed to variations in odor onset or odor rise times per se. Irrespective of potential sources of random and odor-related variance, all statistical effects reported here were immune to such influences, given that the odorants and the stimulus-delivery parameters were exactly the same for the object and valence tasks.

Data analysis—Accuracy was defined as the proportion of responses conforming to the individually determined odor-valence levels and the category membership of the odors. RTs were measured from the onset of the second sniff cue. All RTs were log-transformed to yield normal distributions before further analyses were performed. Hypotheses were tested using repeated measures analyses of variance, with a significance level of $p < .05$, two-tailed. Rate of inhalation at the second sniff was measured on-line; these data were averaged for each individual and task using MATLAB (The MathWorks, Natick, MA; see Fig. 2c for sniff profiles for both the first and second sniff). Because of technical problems, respiratory data were available from only 12 of the 14 participants.

Results

Object evaluation is faster than valence evaluation in a binary task—The critical comparison of Experiment 1 involved testing whether perceptual performance was faster and better during object evaluation than during valence evaluation. Results indicated that binary choices were significantly faster and more accurate during odor object evaluation than during valence evaluation—RT: $F(1, 13) = 15.467$, $p = .002$, $\eta^2 = .543$; accuracy: $F(1, 13) = 13.482$, $p = .003$, $\eta^2 = .509$. These effects were highly consistent across individual participants (Fig. 3). Analysis of respiration revealed comparable inspiration magnitude for the two tasks ($p = .514$).

Because the finding of slower RTs on the valence task could have been driven by trials with low accuracy, we conducted a follow-up analysis in which only trials with odors from different categories were included. Restricting the analyses to these trials increased accuracy on the valence evaluation task (from 69.6% to 80.9%) but had no effect on accuracy on the object evaluation task (from 79.5% to 80.5%), so that accuracy on the two tasks matched ($p = .91$). However, even after we excluded difficult trials to favor performance on the valence task, RTs were faster during odor object evaluations than during odor valence evaluations ($p = .037$). A related analysis equated choice type by restricting the comparison to those conditions that generated a “yes” response (i.e., odors from the same category in the case of the object evaluation task and odors that were more pleasant in the case of the valence task). Again, responses for the object evaluation task were faster ($p < .01$) and more accurate ($p = .023$) than responses for the valence evaluation task. The same profiles were observed when we restricted the comparison to those conditions that generated a “no” response (RT: $p = .002$; accuracy: $p < .001$). Taken together, these results suggest primacy of odor objects over valence, and thus support an object-centered model of odor perception.

A path from object to valence?—Given the temporal precedence of odor objects, it is plausible that the valence of an odor cannot be determined without first extracting information about its object identity. According to an object-centered account, odor object evaluation is a necessary causal step linking stimulus input to valence evaluation. The implication is that RTs for object identification should systematically predict RTs for valence evaluation. To test this prediction, we constructed a two-level hierarchical regression model (using all trials) that predicted RT on the valence evaluation task from RT on the object evaluation task on an odor-by-odor basis (Table 1). The first-level model controlled for subject- and odor-related differences (Bland & Altman, 1995). The second-level model assessed the unique effects of the rated valence difference between the first and second odor in each trial and the RT from the same trial-wise odor pair in the object evaluation task. The results showed that object-evaluation RTs significantly predicted valence-evaluation RTs ($\beta = 0.196$, $p < .001$). In other words, there was a systematic temporal relationship between object and valence evaluation, such that longer object-evaluation RTs were associated with correspondingly longer valence-evaluation RTs. This analysis also demonstrated that smaller valence differences between odors predicted slower valence-evaluation RTs ($\beta = -0.219$, $p < .001$), a pattern consistent with a task-difficulty effect; it was easier to evaluate relative valence for odors differing more strongly along this dimension.

Experiment 2

Together, the results from Experiment 1 indicate that odor valence decisions are delayed by the time it takes to identify the object quality of an odor, as well as by the perceptual similarity of the valence of the compared odors. These findings are consistent with object-centered accounts of odor perception. In a second experiment, we investigated whether the rapid matching of odors to labels is influenced by perceptual odor templates, and whether such matching is susceptible to interference effects from odor valence similarity. If the latter were true, this would provide independent evidence for valence-guided odor identification.

Method

Participants—An independent group of 20 participants (12 women, 8 men; mean age = 23.7 years, *SD* = 2.3 years) with no reported olfactory or health impairments consented to take part in this experiment, which was approved by the Northwestern University institutional review board.

Materials—The stimulus set consisted of eight familiar, moderately intense odorants that were selected to systematically vary in valence and edibility: lemon, almond, garlic, fish, rose, wood, gasoline, and marker pen. Before the experiment, participants rated the valence of the odors. Some odorants were obtained directly from their natural products (gasoline, garlic), and others were obtained as flavors (fish), essential oils (lemon, almond, rose, wood), or monomolecular compounds (marker pen: n-butanol). A laptop computer was used for stimulus presentation and for triggering the olfactometer for odor delivery. Breathing belts were used to measure respiratory patterns throughout the experiment.

Baseline odor testing—Prior to the main experiment, participants were tested for odor detection thresholds (Sniffin’ Sticks, Burghard Instruments, Wedel, Germany; Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997). Across participants, detection thresholds (16 is the highest possible score) were in the normal range (minimum = 7.25, maximum = 16.00; *M* = 13.51, *SD* = 2.42). Participants also provided baseline ratings of the eight odors used in the main task, evaluating their intensity, pleasantness, familiarity, edibility, and perceptual quality (i.e., how well they corresponded to their word labels). These ratings were made on continuous visual analogue scales presented on the computer. The scales ranged from −10 to +10. Each odor was evaluated three times on each of the scales. The procedure was self-paced, with each new trial starting 5 s after the previous rating. The arithmetic mean was calculated for each participant and type of evaluation.

Identification task—On each trial in the main task, a word label was presented during a 3-s countdown preceding the delivery of a single odorant for 1,000 ms; as in Experiment 1, delivery of the odorant was synchronized with the presentation of a sniff cue (red crosshair). Participants were instructed to indicate by button press, as quickly as possible, whether each odor corresponded to the preceding label. The word labels were presented in the following format: “Odor: _____?” with the blank being replaced by “Lemon,” “Almond,” “Garlic,” “Fish,” “Rose,” “Wood,” “Gasoline,” or “Marker Pen.” Only responses from 200 to 5,000 ms following onset of the sniff cue were considered for analyses. Each odor was presented four times, and order of presentation was randomized for each participant. On half of the trials, the label matched the presented odor. Trials were separated by an 11-s stimulus onset asynchrony to limit sensory habituation; the duration of the trial block was approximately 6 min.[1]

---

[1] Participants also completed other tasks (odor detection, odor valence, and odor edibility) that were presented in separate blocks, though these results are not reported here.

Results

Baseline ratings—The odors used in Experiment 2 were perceived as being of high intensity ($M = 5.08$, $SE = 0.56$) and familiarity ($M = 5.01$, $SE = 0.88$), and were well matched to their word labels (i.e., were of high quality; $M = 5.21$, $SE = 0.79$). (Complete baseline ratings of odor intensity, quality, familiarity, valence, and edibility can be found in Fig. S1 in the Supplemental Material available online.) Valence ratings differed significantly across odors ($p < .001$) and conformed to a bimodal distribution with clusters corresponding to pleasant and unpleasant stimuli (see Fig. S2 in the Supplemental Material); thus, the odor stimuli varied widely along this perceptual dimension.

Object templates and valence interference—Performance on the identification task approached ceiling-level accuracy ($M = 94.4\%$, $SE = 0.8\%$), and all recorded responses were included in the analyses of RT. We wanted to test the hypothesis that odor identification decisions would be faster for “yes” responses when an odor was preceded by a matching label than for “no” responses when that odor was preceded by a nonmatching label. The demonstration of faster “yes” relative to “no” responses would suggest the use of odor object templates to enhance task performance, and would be compatible with an object-centered account of olfactory perception. At the same time, we wanted to examine whether valence similarity between the odor cued by the label and the perceived odor itself would interfere with performance on the identification task when the label and odor did not match, which would help to either confirm or refute the valence-centered account. For example, in a valence-centered model, it should take longer to realize that rose odor does not correspond to the cue “lemon” than to realize that rose odor does not correspond to the cue “marker pen,” because the valence responses would be more similar for rose and lemon than for rose and marker pen.

To this end, we constructed a similarity matrix by ranking cued and presented odors in terms of perceived valence, on the basis of each participant’s baseline ratings. In matching trials, cued and presented odors were identical. In nonmatching trials with similar valence of cued and presented odors, the presented odor had a rank-order distance from the cued odor of at most ±2 (in the eight-item list). Trials with a rank-order distance greater than ±2 were categorized as nonmatching trials with different valence. Trials were grouped in this way to ensure that the number of trials was balanced between the two trial types. Faster RTs on matching trials compared with non-matching trials would be congruent with an object-centered account of odor perception. For the nonmatching identification trials, we assessed whether similar-valence trials were associated with longer RTs compared with dissimilar-valence trials, which would be congruent with a valence-centered account of odor processing (see the model in Fig. 4a). Analysis of participants’ ratings confirmed that for nonmatching trials, the valence difference between odor labels and the odors with which they were paired was indeed significantly greater on different-valence trials (e.g., marker-pen cue paired with rose odor) than on similar-valence trials (e.g., lemon cue paired with rose odor; $p < .001$; Fig. 4b).

The matrix projection of the observed RT data (Fig. 4c) indicated that RTs were short on matching trials, but revealed no systematic effect of valence similarity on RTs on nonmatching trials. A repeated measures analysis of variance revealed a significant main effect of trial type (matching, similar-valence non-matching, different-valence nonmatching), $F(1.28, 24.41) = 5.839$, $p = .017$. RTs were faster on matching trials than on similar-valence trials ($p = .023$) and different-valence trials ($p = .017$), but RTs on similar- and different-valence trials did not differ ($p = .811$; see Fig. 4d). The findings indicate that object-specific templates can guide cued odor identification, independently of hedonic semantic information.

Discussion

The temporal cascade of events that begins with olfactory stimulation and culminates in evaluations of odor valence and identity is poorly understood. By using novel olfactory RT paradigms and regression analysis, we found that odor object processing occurs earlier than odor valence processing. Furthermore, object processing times predict valence processing times downstream, but valence similarity between an odor cue and a presented odor does not interfere at the odor identification stage. The demonstration of a priming effect for odor identification on matching trials in Experiment 2 suggests that the formation of object-specific templates may be a mechanism by which the olfactory system optimizes perceptual processing in advance of stimulus receipt (Zelano et al., 2011).

The data presented here favor an object-centered view of olfaction, at least in the context of relatively familiar odors. The new evidence that valence evaluations are relatively slow and inconsistent (see Figs. 3a and 3b) makes it highly unlikely that the valence dimension is the defining feature of olfactory percepts. Thus, odor objects are not defined by their valence, but rather activate emotional responses secondarily. Indeed, odor object activations may function as a requisite relay for perceptual decisions concerning valence. Anatomically, to the extent that odor object representations are likely encoded in piriform cortex (Haberly, 2001; Howard, Plailly, Grueschow, Haynes, & Gottfried, 2009), it is plausible that olfactory hedonic information is extracted only downstream from piri-form cortex, particularly in orbitofrontal cortex, which is the principal olfactory neocortical projection site and is strongly implicated in both animal and human models of odor valence processing and reward value coding (Anderson et al., 2003; Gottfried & Zald, 2005; O'Doherty et al., 2000; Schoenbaum & Eichenbaum, 1995).

Increasing evidence suggests that an odor's valence might be decoded only after its quality is established. Odor novelty induces changes in facial muscle electromyographic activity and heart rate measures earlier than does odor valence (Delplanque et al., 2009). Hedonic evaluations of odors are easily influenced by semantic information (de Araujo, Rolls, Velazco, Margot, & Cayeux, 2005; Herz, 2003), but such influences apparently do not cause confusion in recognition of odor objects. Thus, cognitive factors influence perceived odor valence, but we know of no evidence that changes in valence (e.g., as caused by sensory-specific satiety; see Rolls & Rolls, 1997; Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001) impair recognition of odor objects.

In conclusion, our results support a processing model of odor perception that contrasts with key aspects of valence-centered accounts. Our model suggests that valence is not the defining feature of odor objects, but rather is evoked by these objects. A question of outstanding importance is how varying degrees of access to odor object information influence olfactory valence evaluations. Indeed, the demonstration of object-centered odor perception does not wholly preclude the existence of valence-based odor perception. The contributions of objects and valences to odor perception are likely to depend on the nature of the stimuli, as well as on individual experience. In the case of familiar, easily identifiable odors, such as those tested here, object-centered processes reliably underpin olfactory perception. However, in the case of unfamiliar odors or biologically salient chemosignals that do not readily activate object representations in memory, the olfactory system could provide direct access to affective-motivational systems to optimize behavioral responses. Future behavioral, neuroimaging, and brain-lesion research should help highlight the neuronal networks critical for implementing these perceptual mechanisms.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We thank the members of the Gottfried lab at Northwestern University and Stefan Wiens for making valuable comments on the manuscript, Connie Choi for providing technical assistance, and Johan Lundström for generously donating a fish odor used in the experiment. Jonas K. Olofsson and Nicholas E. Bowman contributed equally to the manuscript. Jonas K. Olofsson, Jay A. Gottfried, and Nicholas E. Bowman designed the research; Jonas K. Olofsson, Nicholas E. Bowman, and Katherine Khatibi performed the research; Nicholas E. Bowman and Jonas K. Olofsson analyzed the data; and Jonas K. Olofsson, Nicholas E. Bowman, and Jay A. Gottfried wrote the manuscript.

Funding

This work was supported by National Institutes of Health grants to Jay A. Gottfried from the National Institute on Deafness and Other Communication Disorders (1R01DC010014, K08DC007653), by a postdoctoral fellowship to Jonas K. Olofsson from the Swedish Research Council, and by a Northwestern University institutional training grant to Nicholas E. Bowman from the National Institutes of Health (T32 AG20506).

References

Anderson AK, Christoff K, Stappen I, Panitz D, Ghahremani DG, Glover G, Sobel N. Dissociated neural representations of intensity and valence in human olfaction. Nature Neuroscience. 2003; 6:196–202.

Bland JM, Altman DG. Calculating correlation coefficients with repeated observations: Part 1—correlation within subjects. British Medical Journal. 1995; 310:446. [PubMed: 7873953]

de Araujo IE, Rolls ET, Velazco MI, Margot C, Cayeux I. Cognitive modulation of olfactory processing. Neuron. 2005; 46:671–679. [PubMed: 15944134]

Delplanque S, Grandjean D, Chrea C, Coppin G, Aymard L, Cayeux I, Scherer KR. Sequential unfolding of novelty and pleasantness appraisals of odors: Evidence from facial electromyography and autonomic reactions. Emotion. 2009; 9:316–328. [PubMed: 19485609]

Gottfried JA. Central mechanisms of odour object perception. Nature Reviews Neuroscience. 2010; 11:628–641.

Gottfried JA, Zald DH. On the scent of human olfactory orbitofrontal cortex: Meta-analysis and comparison to non-human primates. Brain Research Reviews. 2005; 50:287–304. [PubMed: 16213593]

Haberly LB. Parallel-distributed processing in olfactory cortex: New insights from morphological and physiological analysis of neuronal circuitry. Chemical Senses. 2001; 26:551–576. [PubMed: 11418502]

Haddad R, Weiss T, Khan R, Nadler B, Mandairon N, Bensafi M, Sobel N. Global features of neural activity in the olfactory system form a parallel code that predicts olfactory behavior and perception. Journal of Neuroscience. 2010; 30:9017–9026. [PubMed: 20610736]

Herz RS. The effect of verbal context on olfactory perception. Journal of Experimental Psychology: General. 2003; 132:595–606. [PubMed: 14640850]

Howard JD, Plailly J, Grueschow M, Haynes JD, Gottfried JA. Odor quality coding and categorization in human posterior piriform cortex. Nature Neuroscience. 2009; 12:932–938.

Hummel T, Sekinger B, Wolf SR, Pauli E, Kobal G. 'Sniffin' Sticks': Olfactory performance assessed by the combined testing of odor identification, odor discrimination and olfactory threshold. Chemical Senses. 1997; 22:39–52. [PubMed: 9056084]

Johnson BN, Sobel N. Methods for building an olfactometer with known concentration outcomes. Journal of Neuroscience Methods. 2007; 160:231–245. [PubMed: 17081618]

Khan RM, Luk CH, Flinker A, Aggarwal A, Lapid H, Haddad R, Sobel N. Predicting odor pleasantness from odorant structure: Pleasantness as a reflection of the physical world. Journal of Neuroscience. 2007; 27:10015–10023. [PubMed: 17855616]

Klein GS. Semantic power measured through the interference of words with color-naming. American Journal of Psychology. 1964; 77:576–588. [PubMed: 14255565]

Lawless HT. Exploration of fragrance categories and ambiguous odors using multidimensional-scaling and cluster-analysis. Chemical Senses. 1989; 14:349–360.

O'Doherty J, Rolls ET, Francis S, Bowtell R, McGlone F, Kobal G, Ahne G. Sensory-specific satiety-related olfactory activation of the human orbitofrontal cortex. Neuro-Report. 2000; 11:893–897.

Plailly J, Howard JD, Gitelman DR, Gottfried JA. Attention to odor modulates thalamocortical connectivity in the human brain. Journal of Neuroscience. 2008; 28:5257–5267. [PubMed: 18480282]

Plato. Timaeus. Jowett, B., translator. Rockville, MD: Serenity; 2009.

Rolls ET, Rolls JH. Olfactory sensory-specific satiety in humans. Physiology & Behavior. 1997; 61:461–473. [PubMed: 9089767]

Schiffman SS, Musante G, Conger J. Application of multidimensional-scaling to ratings of foods for obese and normal weight individuals. Physiology & Behavior. 1978; 21:417–422. [PubMed: 740758]

Schoenbaum G, Eichenbaum H. Information coding in the rodent prefrontal cortex. I. Single-neuron activity in orbitofrontal cortex compared with that in pyriform cortex. Journal of Neurophysiology. 1995; 74:733–750. [PubMed: 7472378]

Small DM, Zatorre RJ, Dagher A, Evans AC, Jones-Gotman M. Changes in brain activity related to eating chocolate: From pleasure to aversion. Brain. 2001; 124:1720–1733. [PubMed: 11522575]

Smith MC, Magee LE. Tracing the time course of picture-word processing. Journal of Experimental Psychology: General. 1980; 109:373–392. [PubMed: 6449530]

Stevenson RJ, Boakes RA. A mnemonic theory of odor perception. Psychological Review. 2003; 110:340–364. [PubMed: 12747527]

Stevenson RJ, Wilson DA. Odour perception: An object-recognition approach. Perception. 2007; 36:1821–1833. [PubMed: 18283932]

Wilson DA, Stevenson RJ. The fundamental role of memory in olfactory perception. Trends in Neurosciences. 2003; 26:243–247. [PubMed: 12744840]

Wilson, DA.; Stevenson, RJ. Learning to smell: Olfactory perception from neurobiology to behavior. Baltimore, MD: Johns Hopkins University Press; 2006.

Yeshurun Y, Sobel N. An odor is not worth a thousand words: From multidimensional odors to unidimensional odor objects. Annual Review of Psychology. 2010; 61:219–241.

Zelano C, Mohanty A, Gottfried JA. Olfactory predictive codes and stimulus templates in piriform cortex. Neuron. 2011; 72:178–187. [PubMed: 21982378]

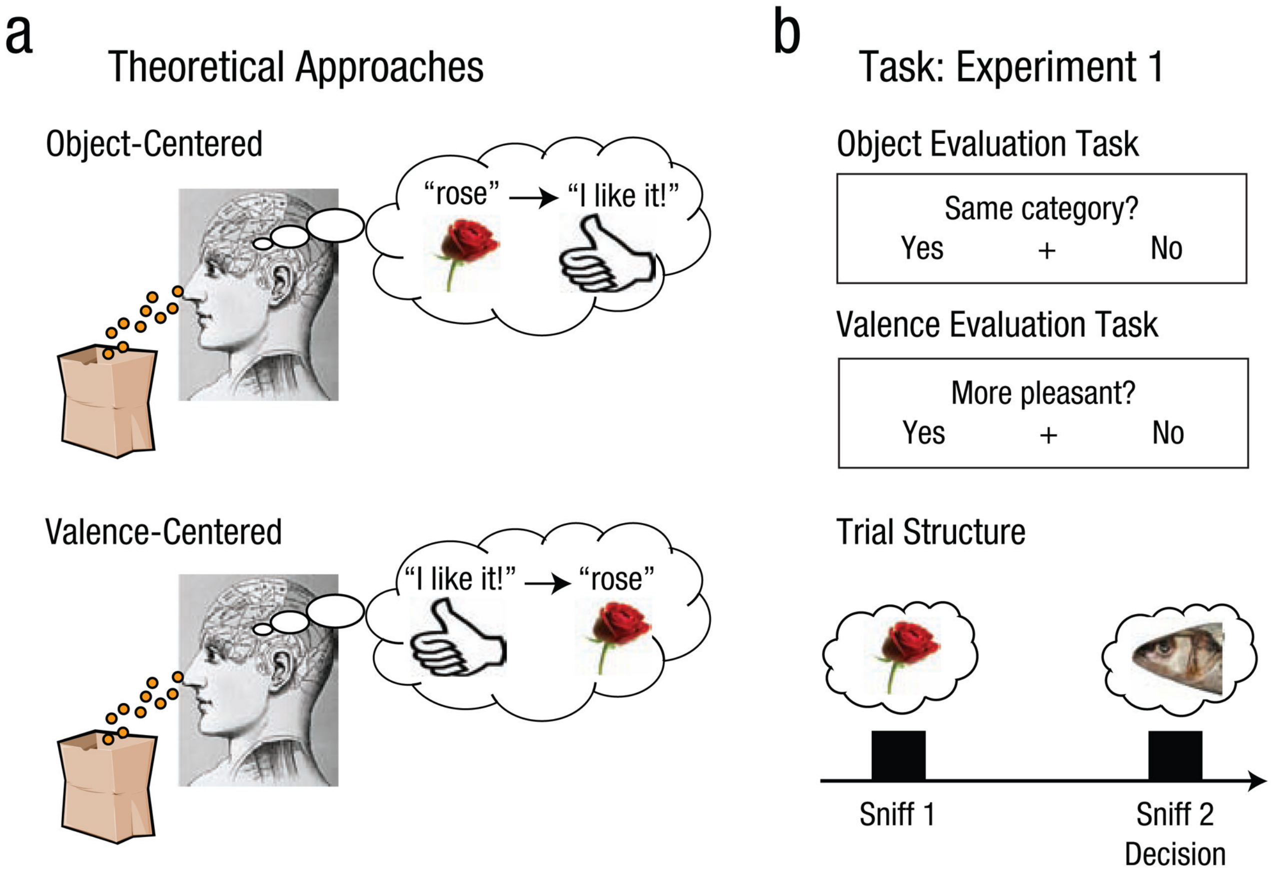

Fig. 1.

Illustration of (a) the theoretical models tested in this study and (b) the decision tasks employed in Experiment 1. According to object-centered accounts, activation of the representation of an odor object (object identification) in turn activates a hedonic response, whereas according to valence-centered accounts, an initial valence determination is necessary for identifying an odor object. In each trial of Experiment 1, two odors were presented sequentially. Participants made speeded binary perceptual decisions via button-press responses, reporting either whether the second smell belonged to the same category as the first or whether the second smell was more pleasant than the first.

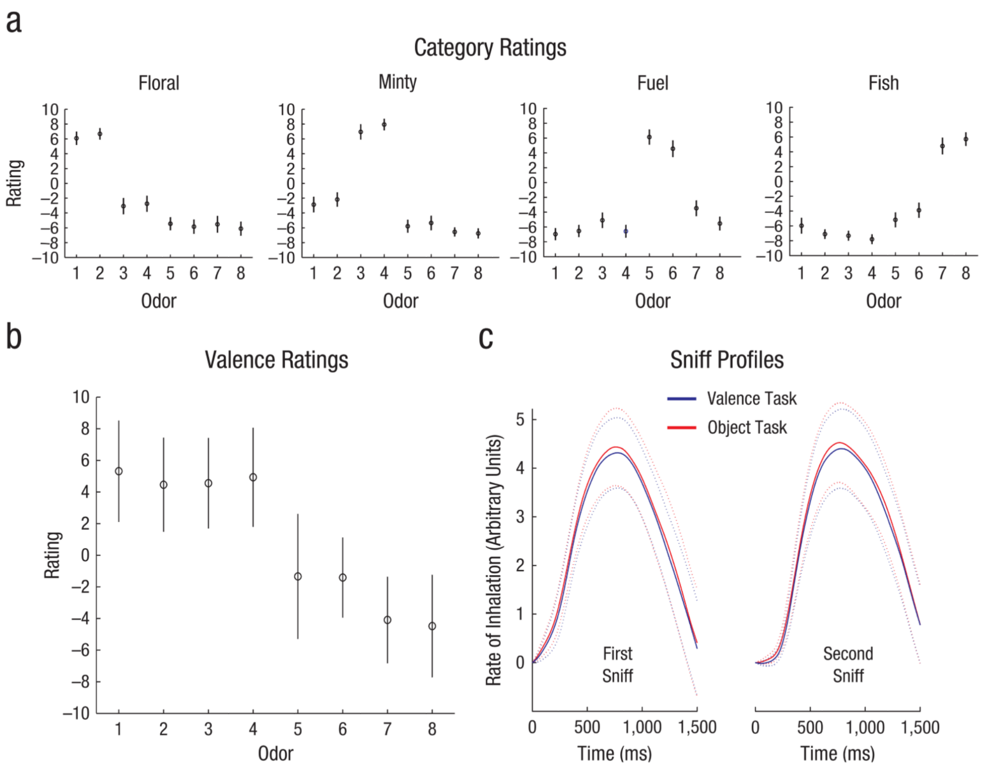

Fig. 2.

Perceptual ratings of the odors and sniff profiles from Experiment 1. The graphs in (a) show participants' mean rating (with standard error) of the extent to which each of the eight odors fit each of the four odor category descriptors (floral, minty, fuel, fish). The graph in (b) shows participants' mean rating (with standard error) of each odor's valence. For ease of presentation, the odors are referred to in the graphs by numbers: 1 = rose; 2 = lilac; 3 = peppermint; 4 = wintergreen; 5 = diesel/motor oil; 6 = gasoline; 7 = sardine; 8 = fish flavor. The graphs in (c) show the sniff profiles (average rate of inhalation as a function of time, with standard error indicated by the dotted line) for the first and second sniffs of each trial, for both the object and the valence tasks.

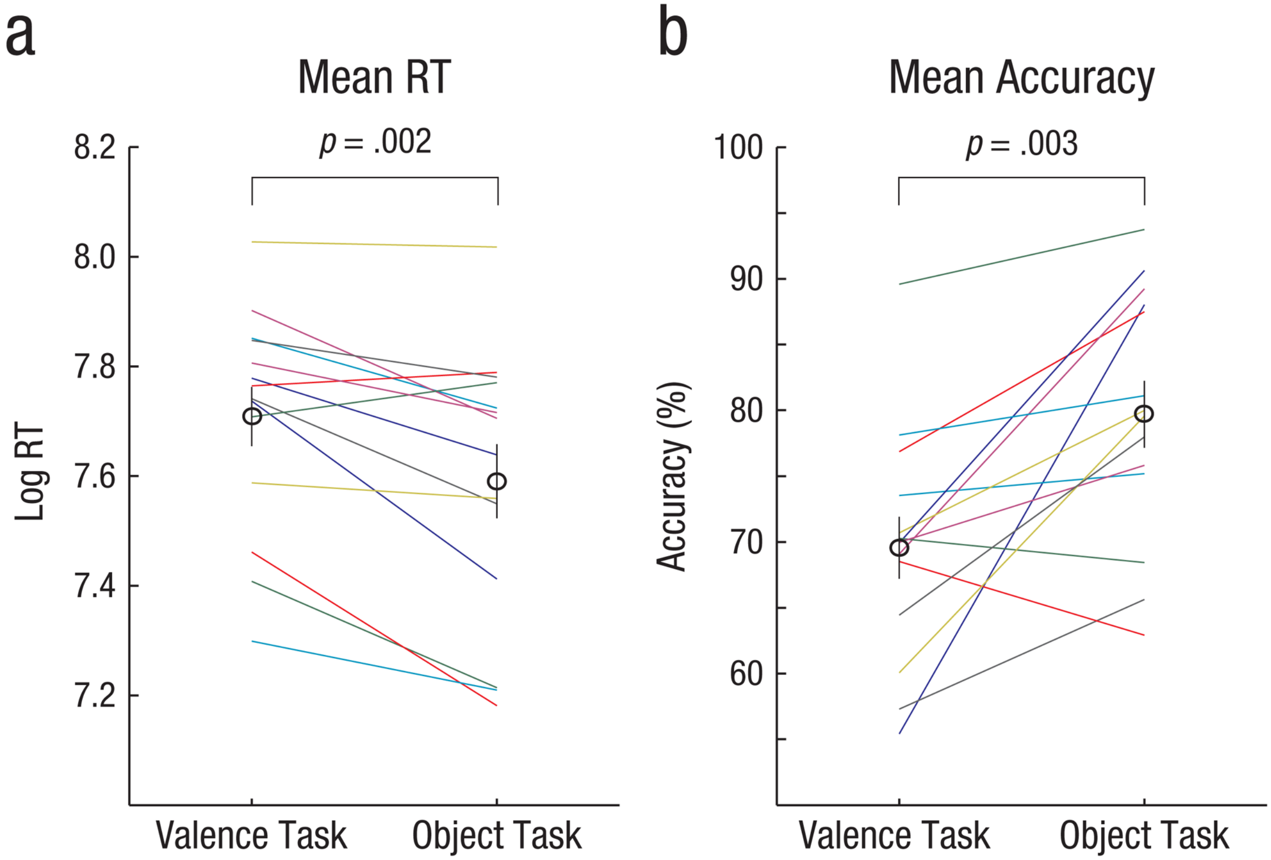

Fig. 3.

Behavioral data from Experiment 1: (a) log-transformed response time (RT) and (b) accuracy on the valence and object evaluation tasks. The colored lines show means for the 14 participants individually, and the black circles show group means, with error bars representing standard errors.

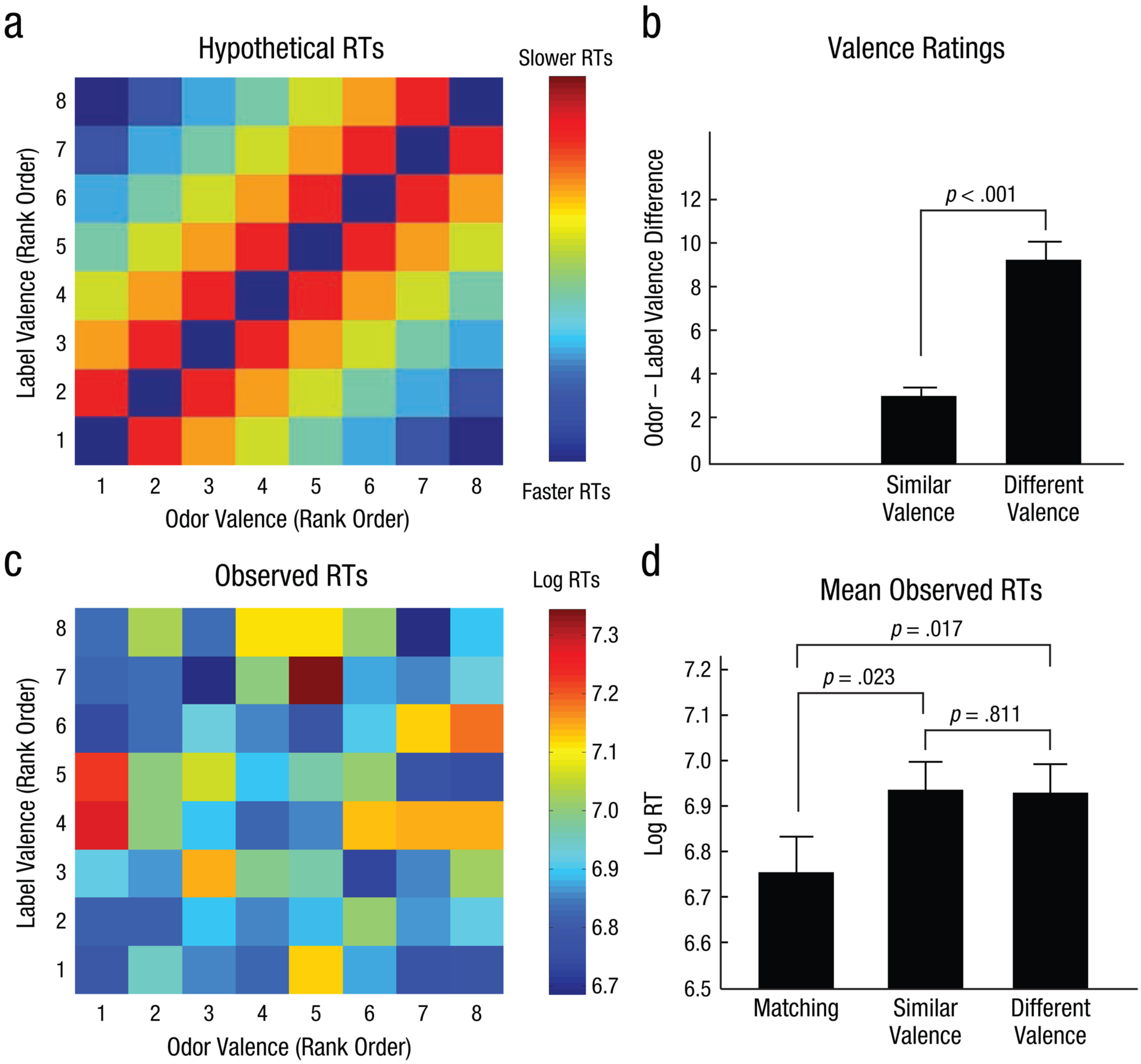

Fig. 4.

Experiment 2: testing the effects of object templates and valence interference on odor object identification. The matrix in (a) shows the predicted response times (RTs) on the identification task for all levels of odor-label similarity, as determined by individual rank orderings of the labels' and odors' perceived valence (1 = most pleasant; 8 = most unpleasant). The color coding indicates predicted patterns in RTs. Facilitation of RTs on matching trials (blue diagonal) would be consistent with perceptual object templates playing a role in odor identification. Valence-centered models predict that valence similarity would interfere with odor identification, such that RTs would be slower for odor-label combinations more alike in valence. The graph in (b) shows the mean difference in valence ratings between odor stimuli and the odor labels with which they were paired, separately for similar-valence trials (combinations coded in red to orange in panel a) and different-valence trials (combinations coded in yellow to dark blue in panel a). Note that on matching trials (e.g., rose cue paired with rose odor), the valence difference was always 0. The matrix in (c) shows observed mean log-transformed RTs for all levels of label-odor similarity, and the bar graph in (d) presents mean RT in the identification task as a function of trial type (matching, similar valence, different valence). Error bars in (b) and (d) represent standard errors.

Table 1

Results of the Hierarchical Regression Analysis Predicting Response Times in the Valence Evaluation Task in Experiment 1

Level and predictor	ΔR^2	R^2	β	*p*
Level 1	.014	.014		
Subject			−0.116	.004
Odor			−0.013	.740
Level 2	.102	.115		
Valence difference between the two odors			−0.219	.000
Object-evaluation response time			0.196	.000